seemed the most probable. Although I shot many in order to procure a female, I only succeeded in getting the one above-noticed, which however I cannot with certainty pronounce to be one. It was shot down from a half-finished nest at more than twenty yards high. Two or three nests are often attached to the same leaf, and twenty or thirty in the same palm. In the beginning of May the newly-hatched young were obtained from a nest, and three quite white eggs from another, although many nests were scarcely half-built.

The notes near the nests were like the warbling and call-notes of the linnet. No song was heard. In the stomach only rice-grains were found, which they were seen to pluck while hopping about the cottages, like sparrows with us. The Bengalese name

is Bawee (the w sounded as in English).

[To be continued.]

XXVIII.—On the Growth of Cell-Membrane. By Hugo v. Mohl*.

[Continued from p. 155.]

When we compare the conclusions necessarily resulting from these calculations with Harting's theory, we see that they are decidedly opposed to it. We have good grounds for the assumption that the mean number, derived from the measurement of ten rows of cells, indicates with tolerable accuracy the course of the normal development of the wood-cells of Hoya carnosa, since the mean numbers already derived from the measurement of five rows of cells differ but very slightly from those above mentioned. If we assume this, it follows that the nearer the intermediate (mittlere) wood-cell (if I may so express myself) of this plant approaches the margin of the wood in consequence of the progressive conversion of the inner cambium-cells into woodcells, the more it enlarges in the radial direction, so that its diameter is $\frac{1}{102}$ of a millimetre when it lies in the second row of cambium-cells (counted from the wood), and when it has advanced to the inner row, bordering the wood, the diameter is increased to $\frac{1}{9.6}$ of a millimetre. According to Harting's view, the cavity of the cell will continue of this size +, since in his opinion the con-

* From the 'Botanische Zeitung,' May 29th and June 5th, 1846. Trans-

lated by Arthur Henfrey, F.L.S. &c.

[†] I here take the diameter of the cavity of the cell as equalling the diameter of the whole cell, which is not altogether right, but deviates little from the truth, since the cambium-cells of *Hoya carnosa* have very thin walls, and as these walls are double, only half this thickness should be reckoned. This is so small a size and one so difficult to give accurately that I thought it might be disregarded; in a measurement which however cannot claim strict ac-

version of the cambium-cell into a wood-cell depends on the deposition of secondary layers upon the outside of the cell; or rather, as was shown above, the cavity of the cell must enlarge in the radial direction in consequence of this external addition of secondary membranes. If we compare with this the size of our intermediate wood-cell, the hypothesis cannot be brought into agreement with its dimensions, for the cavity of the cell lying in the outermost circle of wood diminishes from \(\frac{1}{96}\) to \(\frac{1}{114}\) of a millimetre, while the total diameter of the cell increases to $\frac{1}{7.5}$. These calculations prove beyond a doubt, that in the conversion of a cambium-cell into a wood-cell the cavity is far from remaining of the same size or enlarging; on the contrary, it becomes very manifestly smaller: this can only be accounted for by a deposition of secondary layers on the inside of the primary membrane, or by the assumption of the occurrence of an external compression of the cell-membrane on every side, causing it to occupy a smaller space, for which process no analogy is to be found throughout all vegetable anatomy. That the total diameter of the cell distinctly increases (from $\frac{1}{96}$ to $\frac{1}{75}$ millim.), while at the same time the cavity becomes smaller, is not in the least an objection to the hypothesis that a deposition of secondary layers takes place in the interior of the cell, because there is no reason to prevent our assuming that an elementary organ may increase in breadth, by the intus-susception of new organic matter between the molecules of which its membranes consist, during the deposition of secondary That such a growth is possible and actually does take place, convincing proof is offered by the spiral vessels situated in the interior of the vascular bundle, the spiral fibre of which every one certainly considers as a secondary deposit. This enlargement of the whole cell does not yet attain its maximum while it lies in the most external row of the wood-cells; the above measurements show that in the wood-cells of the second circle the total diameter had increased from $\frac{1}{75}$ to $\frac{1}{71}$, the cavity from $\frac{1}{114}$ to $\frac{1}{100}$ of a millimetre. As seen by these numbers, the total diameter of the cell has increased in a greater proportion than the diameter of the cavity, whence the inference, that simultaneously with the enlargement of the cell, a thickening of its walls takes place, which however is not quite sufficient to hinder the enlargement of the cavity of the cell, by the expansion of the cell-wall.

If from this refutation of the reasons adduced by Harting in favour of the external addition of the secondary layers, founded on micrometrical measurements, we pass to an anatomical exa-

curacy, the thickness of the walls parallel with the wood of the cambium-cells of Hoya amounted to at all events not more than $\frac{1}{2500}$ of a millimetre, if anything less.

mination of the wood-cells themselves, their structure affords decided proof, that secondary layers are deposited upon the inside of the primary membrane. The analogy between the structure of the wood-cells and that of parenchymatous cells, as for instance the cells of horny albumen, the dotted, thickwalled medulla- and bark-cells of Hoya carnosa, in which Harting himself does not deny an internal growth, at once offer reasons not to be disregarded, for the assumption of an analogous process of development in the two kinds of cells. Where the anatomical relations of the individual layers are so perfectly analogous, it would require very clearly-ascertained facts to induce us to assume that nature follows a different law of formation in the wood-cells from that which obtains in the parenchymatous cells, and of such facts I have no knowledge. On the other hand, the history of the development of prosenchymatous cells affords in my opinion very certain evidence of the contrary. In relation to this perhaps there is nothing so instructive as the examination of the cells of the Conifera, and I believe that a conclusion deduced from these elementary organs will hold good in reference to the wood-cells of Dicotyledons, since spiral fibres on the inner surface of the cell, together with a bordered dot, resembling those occurring in Taxus, are also found in many wood-cells, as for instance in Viburnum Lantana. Now the examination of young shoots of Pinus sylvestris (and exactly in a similar manner also, the examination of young dotted vessels of dicotyledonous wood) affords evidence that the cavity which subsequently forms the border of the dot, and which is situated between the outer closed membranes of two contiguous cells, appears very early, while the cell-membrane is yet very thin, and is in every case already perfectly formed at a period when no trace can be seen of the dot, leading to the cavity, situated in the inner layer of the cell. It does not admit of the slightest doubt therefore, that the outer closed membrane of the cell is the primary, and that the inner layers which are perforated by the canals of the dots are subsequently deposited upon the inner surface of the primary membrane.

It is not here meant to be denied that deposits do occur upon the outer side of the primary membrane in many cases, for instance in this very wood of *Pinus sylvestris*. This takes place in the intercellular passages which are found between the cells while their walls are still thin, in which an intercellular substance is deposited; but this has nothing to do with the thickening or growth of the cell-membrane.

Although in the foregoing remarks, I have been forced, in the defence of my theory, to repel many of the objections advanced by Harting and Mulder on anatomical grounds, because I cannot

acknowledge as accurate the observations upon which they are founded, it is otherwise with the objections which those observers have brought forward in a chemical point of view, since I do not indeed differ from them as to the facts they mention, but cannot agree with the conclusions they have thence drawn.

Although Harting and Mulder are not themselves always of the same opinion in reference to the chemical constitution of the compounds found in the cell-wall, yet in regard to the history of development of the cell-wall they draw similar conclusions from their joint investigations, so that I can here take their objections together. The most important points coming under consideration

are the following:—

The wall of young cells consists in general of cellulose alone, it being coloured blue by iodine and sulphuric acid; in older cells on the contrary, which possess thickened walls, distinct layers may usually be distinguished, differing chemically. In the wood-cells, bark-cells and milk-vessels, the outermost layer (external woodmembrane of Mulder; cuticle of the wood-cell of Harting) consists of a substance wholly insoluble in sulphuric acid. That this membrane is produced after that which is composed of cellulose, is evident from the circumstance that the young wood-cells acquire the blue colour in every part; the outer membrane is therefore considered by Harting and Mulder as a layer deposited on the outside of the membrane composed of cellulose. From the relation of this outer membrane to the first-formed pores, Harting derives the variations of the canals of the dots: when the outer membrane is produced in proportionately more abundant quantity and spreads itself between two cells, over their whole surface, the pores become closed; if, on the contrary, this membrane be only deposited in the same proportion as the cells increase in breadth, the pores remain open; if, lastly, its development do not keep pace with the expansion of the cell, a cavity is produced between the dots. From the circumstance that in the full-grown cell the layer of cell-membrane surrounded by this outer membrane is usually no longer coloured blue by iodine and sulphuric acid, but this colour, even when it appears at all, is only to be found in the inmost layer bordering the cavity of the cell, while the remaining portion is coloured either vellow or green, it is further deduced, that these intermediate layers of the cell (Mulder's intermediate ligneous substance), which take a yellow colour with the reagents mentioned and are soluble in stronger sulphuric acid, have been deposited, at the same time as the outermost layer, in the direction from within outwards. Mulder's and Harting's views however do not wholly agree in reference to the formation of this layer. The former assumes, that either the cellulose is wholly absorbed and becomes replaced

by this intermediate ligneous substance, or that the intermediate ligneous substance is deposited on the outside of the oldest and innermost layer (the cellulose); while Harting assumes that this encrusting matter does not replace the cellulose, but permeates the cell-wall composed of cellulose from within outwards and accumulates in preference in its outer layers. This intermediate ligneous substance is always combined with proteine. As analogous to this deposition of intermediate ligneous substance, as the intermediate layers of wood- and bark-cells and as the outer layer of medulla-cells (in which latter Mulder did not find the outer ligneous layer), other encrusting matters occur in the cells of particular organs, for instance pectose in the so-called Collenchyma, and in the milk-vessels a substance partly isomerous with vegetable mucilage, partly with cellulose, in the cells of the horny albumen of Alstræmeria, Iris, Phytelephas, &c.

The conclusion which Harting and Mulder draw from the chemical facts here mentioned, with regard to the development of cell-membrane, goes to establish the opinion, that those layers, which in the membrane of a full-grown cell are characterized by a peculiar chemical reaction, not yet presented by the membrane of young cells, have been formed subsequently to the membrane, consisting of cellulose, of the young cell, and that since these layers occur on the outside of the full-grown cell (the inmost layer of which is composed of cellulose, and therefore corresponds to the membrane of the young cell), the cell-membrane has increased in thickness in consequence of the subsequent deposition

of layers, differing chemically, from within outwards.

Let us examine whether these conclusions be not too hasty. It does not admit of the slightest doubt, that the chemical compounds which are coloured yellow by iodine and sulphuric acid, and which characterize the outer and intermediate layers of most full-grown cells, are of later origin than the cellulose which forms the membrane of the young cell. From this fact however it is a great leap to the assumption, that these layers, which are composed of a substance differing from cellulose, are in reference to their situation also newly-formed layers, which are wanting in young cells. This is quite possible; but it is also possible, that the fact as shown by anatomy is altogether otherwise. If we first of all disregard totally the above distinct anatomical facts, we may, with quite equal right to that by which an external formation of a new layer is inferred, guess, that in a layer of the cell originally consisting of true cellulose, subsequently, and without any alteration of its relations of position, the cellulose is absorbed and replaced by an essentially different chemical compound; or that the cellulose remains and a new compound is deposited between its molecules, and prevents more or Ann. & Mag. N. Hist. Vol. xviii.

less completely the reaction of cellulose, which this in its normal condition exhibits towards iodine and sulphuric acid. an infiltration might perhaps occur without visible thickening of the layer, either if it were not in very great abundance, or if the growth of the membrane in a lateral direction connected with development of the cell were to afford space for the deposit of a considerable quantity of a foreign compound. In these cases, the possibility of which in the first place certainly no one will call in question, a layer would indeed be formed altogether new in a chemical aspect, but no alteration in anatomical relations would appear; and from this subsequently-resulting chemical transformation no conclusion should be drawn as to the order in which the different layers of the cell-membrane originate, since these metamorphoses may take place quite as readily in the last as in the first formed layer*. If we admit the possibility of such a metamorphosis in particular layers, it must also be admitted that the chemical reaction of a certain layer affords no sure means by which it may be recognised as a peculiar anatomical layer, since it may easily be imagined, that in different cells, the layers corresponding to each other in an anatomical point of view may exhibit a great distinction in regard to their chemical transformations. Until well-grounded experience has taught us which of the cases, which have here been mentioned as possible, really occurs in nature, we can only allow ourselves to be guided in the recognition of the different layers and the determination of the order in which they make their appearance by their anatomical relations; and although in very many cases the influence of chemical reagents affords an excellent means by which we are enabled to distinguish the individual layers of cell-membrane, which without this assistance it would be difficult or impossible to recognise, yet in availing ourselves of this assistance we must keep the anatomical relations constantly in view.

The consideration of these relations leads one, I believe, to a result diametrically opposed to that maintained by Mulder and

Harting.

In the next place will come conveniently the question, whether the outer wood-membrane is produced out of a cellulose membrane, or is deposited on the outside of an already formed cell. This membrane exhibits the most striking contrast to the membrane composed of cellulose; if it can be proved to owe its origin to the transformation of a cellulose membrane, the much slighter

^{*} This is no mere guess, as in the parenchyma-cells of some Fern stems, especially of *Polypodium incanum*, *P. nitidum*, the inmost layer of the cell, an analogue of their primary membrane, is far richer in a substance coloured yellow by iodine than the intermediate layer, and requires a much stronger action of sulphuric acid for the production of a blue colour.

differences which distinguish the secondary cell-membranes from true cellulose will appear to us of less consequence. This proof however, in my opinion, the outer wood-membrane furnishes the most clearly of all. I have already, reasoning on the examination of the wood of Pinus sylvestris, on anatomical grounds, shown the outer membrane to be the primary; chemical examination of young cells does not contradict this, since at the time when the borders of the dots are already perfectly formed, but neither the dots themselves nor the inner layers in which they are situated yet exist, the membrane of these cells is coloured by iodine and sulphuric acid, not yellow, but blue. The relation of the membrane to the borders of the dots leaves no doubt that we have here to do with the same membrane which subsequently appears as the outer layer of wood with wholly altered chemical properties. We must therefore assume, that the cellulose of which this membrane originally consists is either absorbed and replaced by the substance of the outer ligneous layer, or that the latter penetrates into the cellulose and prevents its reaction towards iodine and sulphuric acid. Which of these cases occurs, cannot be decided until some solvent for the substance of this membrane shall be found which will not at the same time dissolve the cellulose, yet remaining in it, or at least will give some evidence of its presence. Since such a solvent is not yet known, the question must for the present remain open; perhaps the following observations may afford a hint.

I tried next whether the action of stronger sulphuric acid on the outermost layer of membrane of the wood-cell, especially in the Conifera, would produce a blue colour, but did not in this way attain my object. The formation of the blue colour depends therefore on the simultaneous reaction of sulphuric acid, iodine, water and cellulose. If concentrated sulphuric acid be applied, the cell-membranes do not become blue so long as the necessary water is wanting; or if they be already coloured blue, this colour is soon lost again, and the secondary layers become dissolved. This solution however affords no convenient means by which to obtain the outer membrane isolated, and to examine the colour which, after the action of a stronger acid, it assumes with iodine and weak acid, since so soon as water and tincture of iodine are added to the fluid in which the preparation lies, the dissolved cellulose is precipitated again of a very dark blue colour, and envelopes the outer membranes in such a manner, that no certain conclusions can be drawn as to its colour. I sought therefore to separate the outer membrane from the secondary layers before I applied the sulphuric acid to it. This may always be done in the fibres of the liber of the black fibrous wood of the Palm which is imported from Brazil for the manufacture of sticks,

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&c., as the liber-cells may easily be detached from each other if the vascular bundles have been kept for some time in dilute nitric acid, by which means the outer membranes of the contiguous cells are not separated from each other, but from the secondary membranes, and may be obtained isolated in large pieces. With iodine and sulphuric acid of a degree of concentration which does not dissolve the secondary membranes, but colours them bright blue, this outer membrane behaves exactly like the outer membrane of the wood-cells of dicotyledons, that is, it does not swell up, but acquires a dark yellow colour. If we apply stronger sulphuric acid, capable of completely dissolving the secondary layers, the outer membrane, without any perceptible expansion, acquires either an intense greenish or tolerably pure blue colour. This contains cellulose also, but in what I may call a much more strongly combined condition than is the case in the secondary layers, so that not only is a far stronger acid necessary to bring out the blue colour, but the cellulose present in this membrane is also protected from solution. This greater resistance to the action of sulphuric acid clearly can only depend upon the presence of the substance which acquires the yellow colour with iodine and sulphuric acid. This resistance however has a certain limit, since this membrane is soluble in more concentrated sulphuric acid. It differs therefore in reference to this last circumstance from the outer membrane of the wood-cells of dicotyledons, which resists the action even of the more concentrated sulphuric acid. To try therefore whether cellulose might not be discovered in the latter by the action of a stronger acid, I submitted the wood-cells of various Coniferæ, particularly of Pinus sylvestris, to a similar treatment with nitric acid, &c. The experiment succeeded but imperfectly. After the action of a strong acid, the outer membrane exhibited throughout a greenish colour, but the development of the blue colour was so weak, that I remained in doubt whether it was actually situated in the outer membrane itself, or whether possibly it was not to be ascribed to a thin layer of adhering cellulose. I place no weight therefore on this experiment, and mention it here chiefly to invite others to direct their attention also to this point.

The following observations made on Ferns appear to me to bear more importantly upon the theory of the development of cell-membrane:—The brown cells which in Ferns form the layer by which the vascular bundles are surrounded, withstand the action of sulphuric acid as obstinately as perhaps any other vegetable tissue. In many Ferns all the walls of these cells do not possess a brown colour, but merely those portions of the walls lying upon the vascular bundle, or these and the side walls, while the side turned away from the vascular bundle is unco-

loured, and reacts like cellulose with iodine and sulphuric acid. The brown-coloured walls are usually much thicker than those consisting of cellulose. Leaving the brown colour out of view, these cells correspond exactly, in respect to form and their behaviour toward iodine and sulphuric acid, with the epidermiscells of many leaves. Similar cells occur in the parenchyma of the stem of Polypodium nitidum, Kaulf, some isolated, some in groups of three or four, scattered among the parenchyma-cells, which are usually composed of cellulose; in these cells also one wall is generally thinner and formed of cellulose, while the remaining walls are very thick and brown, and withstand sulphuric acid. All sides of these cells are finely dotted, as is also the case in the cells of the brown coat inclosing the vascular bundle; the dots penetrate as well in the thickened brown as in the thin walls, from within outward to the thin outer and imperforate membrane, which membrane possesses the same chemical peculiarities as the secondary layers lying behind it; that is to say, it consists sometimes of cellulose, at others of a substance withstanding sulphuric acid. Now I found, both among the cells scattered in the parenchyma and in the brown layer inclosing the vascular bundle, particular cells, which certainly, in reference to their form, though not in regard to their chemical characters, wholly agreed with neighbouring brown cells, in which therefore one wall was also thin and the rest considerably thickened. some parts all the walls of these cells, both thick and thin, consisted of cellulose; in other parts the thickened walls were only composed of the brown substance in one point, while the remaining portion, transversely through the whole thickness of the cellwall, consisted of cellulose; the line of demarcation between the brown and the uncoloured portions was not distinctly defined. From the piecemeal composition of the cell-walls of tracts formed of cellulose, and others consisting of brown substance, it clearly results that the greater thickness which the brown walls of these cells usually possess, compared with the walls consisting of cellulose, is neither to be ascribed to the deposition of membranes upon the outside of the young cellulose membrane, nor to the interposition of a considerable mass of brown substance between the molecules of the cellulose, since if the formation of the thickened brown walls depended on these causes, the portions consisting of cellulose could not have exhibited the same thickness and form as the coloured portions in the only partially browncoloured cell-walls. The reason of the brown colour therefore, and of the altered chemical behaviour, must be looked for in a transformation of the whole substance leaving the form and organization of the cell-wall unchanged, or in the infiltration of a

foreign matter in a quantity very small in proportion to the cellulose.

I thought it necessary to enter more minutely into the description of these cells, because they offer the clearest evidence that the presence of a compound differing chemically from cellulose in a thickened cell-wall, even when traces of cellulose can no longer be detected in the membrane by iodine and sulphuric acid, affords no sufficient ground for the assumption that the thickening of the wall depends on the deposition of an incrusting substance, and that we have to regard those portions of the cell-wall formed of this substance as produced subsequently to the portions which are composed of cellulose. Were the incrusting substance, situated at particular points, to penetrate through the whole cell-wall (primary and secondary membrane) in these cells, the extent to which it spread would include the outer layer of the cells, so that this layer would possess all the peculiarities of the outer wood-membrane, and it would thus exactly fit all the conclusions respecting this membrane which Mulder and Harting have drawn; on the other hand, it is not necessary to indicate more minutely how false would be the as-

sumption of its originating subsequently.

The organization of the above-described cells of *Polypodium* nitidum appears to me to be of importance in so far as it is capable of warranting our conclusions as to the structure of epidermis-cells and cuticle, which corresponds with it exactly in an anatomical point of view. Some years since * I stated the anatomical grounds which prevented my regarding the cuticle as a layer secreted upon the outside of the epidermis-cells, and which testified that it consists of the thickened outer walls, and partly also of the side walls of the epidermis-cells, the substance of which has become capable of resisting sulphuric acid in consequence of a peculiar metamorphosis. This explanation does not appear to have met with a favourable reception, but renewed researches have caused me to persevere in my view, and it appears to me to be especially proved by such cases as where the cuticle of canals of dots is continued out from the cavity of the epidermis-cell (as in the leaves of Hakea gibbosa), or where the side walls of the epidermis-cells are dotted and possess the same chemical peculiarities as the cuticle (e.g. in Hakea gibbosa, H. pachyphylla, Hoya carnosa), where also undoubted primary and secondary membranes in a similar manner exhibit the chemical characters of the outer wood-membrane; lastly, such cases as where the primary membrane of the side wall in that half which is directed toward the upper surface of the leaf

^{*} Linnæa, t. 16. Verm. Schriften, 260.

possesses the chemical peculiarities of cuticle, and that half, on the other hand, which is contiguous to the parenchyma of the leaf, the characters of cellulose (e.g. in Hoya carnosa, Aloe obliqua, margaritifera). In all these cases cells present themselves to us, the walls of which, either in certain situations or throughout their whole extent, withstand sulphuric acid, and in which no cellulose is to be discovered. The analogy which exists between these cells and the above-described cells of Polypodium nitidum appears to me to be of importance to the explanation of these latter circumstances. If it be certain in these last, that their membranes, notwithstanding that no cellulose is any longer to be demonstrated in them, nevertheless have their origin from a cellulose layer which exhibits exactly the same organization and thickness as the incrusting membrane, and in many cases still forms particular parts of the membrane, not even then must the conclusion be drawn in respect to the cuticle from its chemical constitution, that it is a layer secreted upon the upper surface of the epidermis-cells, until it can be demonstrated that this theory is in accordance with the anatomical phænomena, and that the instances I have given of a composition of cuticle from cell-membranes, and of the occurrence of epidermis-cells with side walls, partly consisting of cellulose and partly of the substance of cuticle, are founded upon false observations.

Whether now in these cases the cellulose is partly or wholly absorbed and replaced by the incrusting matter, or whether its reaction to iodine and sulphuric acid is merely prevented by the latter, is uncertain. It appears however to me not improbable that the latter is the true view, since the assumption that incrusting substance coloured yellow by iodine and sulphuric acid at least to a certain degree interferes with the known reaction of cellulose, supported not only by the above-mentioned behaviour of the outer layer of the liber fibres of a Palm and of the wood-cells of Pinus sylvestris, but also by the behaviour of the secondary layers in almost all full-grown wood- and parenchyma-cells. Young cells, for instance the pith of a young shoot of Sambucus nigra, the cambium-cells of dicotyledons, &c., become coloured bright blue by the application of a very dilute acid, while the medulla-cells of a full-grown branch of Sambucus and the perfect wood-cells, treated with the same acid, only develope a yellow colour and require it much more concentrated, and then as deep a blue colour is not produced, on account of the yellow colour of the incrusting matter mixing with and rendering it green. A bright and intense blue colour can usually only be obtained in the secondary layers of full-grown wood-cells when so strong an acid is employed that they do not merely swell up but are partially dissolved; in this case the dissolved portion is precipitated in combination with iodine, if the acid be diluted with water, of a splendid and intense blue colour, while the portion of the membrane, the organic structure of which has not been destroyed, although it has undergone a considerable breaking up, exhibits the blue colour but weakly in proportion, and frequently appears green on account of the preponderating intensity of the yellow colour. Since in this manner a perfect destruction of the organization of the secondary incrusting layers renders it possible for the reaction of cellulose toward iodine and sulphuric acid to manifest itself, it is certainly conceivable that in cases where the sulphuric acid is not in a condition to affect a membrane, cellulose may be present in it, but be protected from the action of the acid by the incrusting matter, and thus rendered imperceptible.

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